

# THE CYTOGENETICS OF POA PRATENSIS<sup>1</sup>

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## INTRODUCTION

*Poa pratensis* L., the common Kentucky Blue grass, is universally recognized by taxonomists as an extremely variable species. Many different strains are included within the species, and although American botanists do not generally recognise them as being sufficiently distinct to warrant their segregation from *pratensis* they are conspicuously present. Basic information on their variability, inheritance, and methods of reproduction would not only make it possible to classify the various strains more efficiently but it would allow us to use the species to best advantage for pasturage, turf, etc. It would also indicate what improvements might be expected by breeding for superior strains and the methods to be followed in making such improvements.

In this investigation an attempt has been made to correlate data from morphological, cytological, and genetical studies in an effort to arrive at a clearer understanding of the behavior of the species.

## MATERIALS AND METHODS

Materials for this study have, for the most part, come from the Missouri Botanical Garden Arboretum, Gray Summit, Missouri. In the spring and summer of 1941 additional data have been obtained from plants growing in the nurseries of the United States Golf Association, Green Section, at Arlington, Virginia. Most of these plants came originally from estab-

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lished turf selected at various places throughout the United States.

At the Missouri Botanical Garden Arboretum eleven lots of seed from well-established clones were harvested in 1939, all being taken from open-pollinated panicles. The parent clones varied in width from 1 to 3 feet and were growing in an area approximately 50 feet square. There was therefore considerable opportunity for cross-pollination between clones. Seed was sown in the greenhouse the first week in January 1940. In February individual plants were transferred to 2-inch pots and removed to a cool greenhouse. They remained here until April, at which time they were moved to the nursery.

Both permanent and smear methods have been employed in cytological studies. La Cour's 2 BD fixative was used in all cases where permanent preparations were desired. The Feulgen staining technic, supplemented by crystal violet and acetocarmine, was used to advantage.

#### PROGENY ANALYSES

*G.S. Lot 1.*—Seeds from open-flowering panicles were collected from a single clone in 1939. The resulting progeny was analyzed after two year's growth, i. e., after the plants had reached full maturity. Of 133 plants in the family, 131 were uniform and morphologically closely resembled the mother parent. These were of tall upright habit, possessing relatively narrow leaves and average-size panicles. The two aberrant plants were easily distinguished by their low habit of growth, darker green color, and wider leaves.

*G.S. Lot 2.*—In this lot 103 plants were grown to maturity, 102 of which were morphologically constant and indistinguishable from the female parent. They resembled those of Lot 1 very closely and were definitely of the "hay" type. They were tall, with narrow leaves and panicles of medium size. The one aberrant plant was a low, spreading type with wide leaves and a heavy inflorescence. It resembled somewhat the "off types" in Lot 1, but deviated from the maternal parent even more than the aberrants of the first lot.



*G.S. Lot 3.*—Of the 100 plants composing this progeny all were absolutely uniform, with growth habit and morphology resembling closely those of the first two lots.

*G.S. Lot 4.*—These plants represent a type very different from those of the previous lots. They are characterized by low growth, light green leaves, and small purple inflorescences. Fifty-five seedlings were raised to maturity, all of which were absolutely uniform and indistinguishable from the maternal parent.

*G.S. Lot 5.*—The parent of this lot of plants was of tall upright growth habit. The leaves were slightly more than medium width and dark green in color. Panicles were of average size. Progeny of this parent, consisting of 55 plants, may be segregated into two distinct classes: (1) those identical with the parent, to which class belong 45 of the plants; (2) 10 plants with lax, glossy, light green leaves almost twice as wide as those of the parent, and inflorescences extremely long and heavy. By observation alone one could easily place each of the plants into one of these two classes. No intermediates occurred.

*G.S. Lot 6.*—Of the 60 plants comprising this selection, all were uniform with the exception of some slight differences in time of flowering. However, this variation can hardly be referred to as of a genetic nature since it might easily be the result of soil heterogeneity, differences in soil moisture or disturbances from cultivation.

*G.S. Lot 7.*—This progeny, consisting of 60 plants, was of a type almost identical with Lot 1. They were strikingly uniform throughout and showed no morphological deviation from the parents.

*G.S. Lot 8.*—As a whole, these plants resembled the aberrants of Lot 3. They are characterized by tall culms, wide, lax, light green leaves, and very long panicles. The progenies were surprisingly uniform and, with one exception, quite similar morphologically to the maternal parents. The one aberrant in a progeny of 60 plants possessed stiff, narrow, dark green leaves and a small, almost dwarfed inflorescence.



*G.S. Lot 9.*—The 60 plants grown to maturity were uniform throughout and indistinguishable from the maternal parent.

*G.S. Lot 10.*—The plants from which seed for this progeny was collected were characterized by low, spreading growth and very vigorous habit. The leaves were wide (5–6 mm.) and dark green in color. Panicles were large, heavy, and late-flowering. Fifty of the 60 seedlings closely resembled the female parents morphologically, while the other 10 were variants. However, as has been shown for Lot 5, the variants were quite uniform among themselves. All 10 plants fell into a class characterized by narrow leaves and small panicles.

*G.S. Lot 11.*—These plants were typical “hay” type with tall upright growth, moderately narrow leaves and average-size panicles. The parent clone was of this general type and 53 of the 55 plants grown from seed were almost identical with the parent. The two aberrants differed markedly from the typical plants. They were a low, spreading, wide-leaved type with very long heavy panicles.

TABLE I  
SUMMARY OF MORPHOLOGICAL VARIATION IN GRAY SUMMIT PROGENIES

	Number of plants	Number of aberrants	Per cent aberrants
G.S.- 1	133	2	1.50
G.S.- 2	103	1	0.97
G.S.- 3	100	—	—
G.S.- 4	55	—	—
G.S.- 5	55	10	18.18
G.S.- 6	60	—	—
G.S.- 7	60	—	—
G.S.- 8	60	1	1.66
G.S.- 9	60	—	—
G.S.-10	60	10	16.66
G.S.-11	55	2	3.63

All the plants described in the foregoing paragraphs were obtained from seed collected from open-pollinated panicles. With the exception of Lots 5 and 10, these progenies have been quite uniform and very similar to the maternal parents.

The Arlington plants were subject to a somewhat different



method of study. The seed had been harvested from single isolated plants in nursery rows. Collection was made not only from open-pollinated panicles but from inflorescences that had been isolated from foreign pollen by bagging prior to anthesis. In some instances seed-setting in parchment isolation bags was very poor, but enough seed was always produced for progeny analyses. Seedlings were started in the greenhouse and then transferred to nursery rows. Those from free-flowering and isolated panicles of the same plant were placed in adjacent rows for comparison. At the height of their flowering season they were analyzed morphologically in the same manner as were the G.S. progenies.

The contrast between progenies from isolation and open-pollination was sometimes very marked (pls. 28-29). For example, B-2 after open-pollination produced a uniform and maternal-like progeny typical of apomictic strains. The selfed progeny of this line, however, showed a degree of variation that might be expected only from sexually reproducing plants. Even before flowering, distinct differences between plants could be easily ascertained from vegetative characters, the variability in leaf width being especially noticeable (figs. 1 and 2). At the time of flowering distinct differences in the inflorescences, including size of panicles, number of florets per spikelet, etc., were evident. There also occurred in the selfed line of this progeny a number of weak plants, many of which did not survive beyond the seedling stage. Other weak plants which were grown to maturity exhibited characters entirely foreign to *P. pratensis*.

Another example of very distinct differences in open and selfed lines of the same strain is provided by selection B-6. Here also the progenies grown from open-pollinated panicles were uniform and exhibited a tall upright habit of growth (pl. 28). The progeny produced after isolation, although not quite so variable as the selfs in B-2, was of an entirely different growth habit from that produced after open-pollination, almost without exception being low-growing, spreading, semi-decumbent types (pl. 29).



In contrast to the B-2 and B-6 seedlings, those of B-17 and B-1 showed absolutely no differences between open and selfed lines, and all were essentially maternal-like in appearance (pls. 26 and 27).

In addition to the three strains mentioned above, progenies of open and selfed lines of eleven other selections were grown

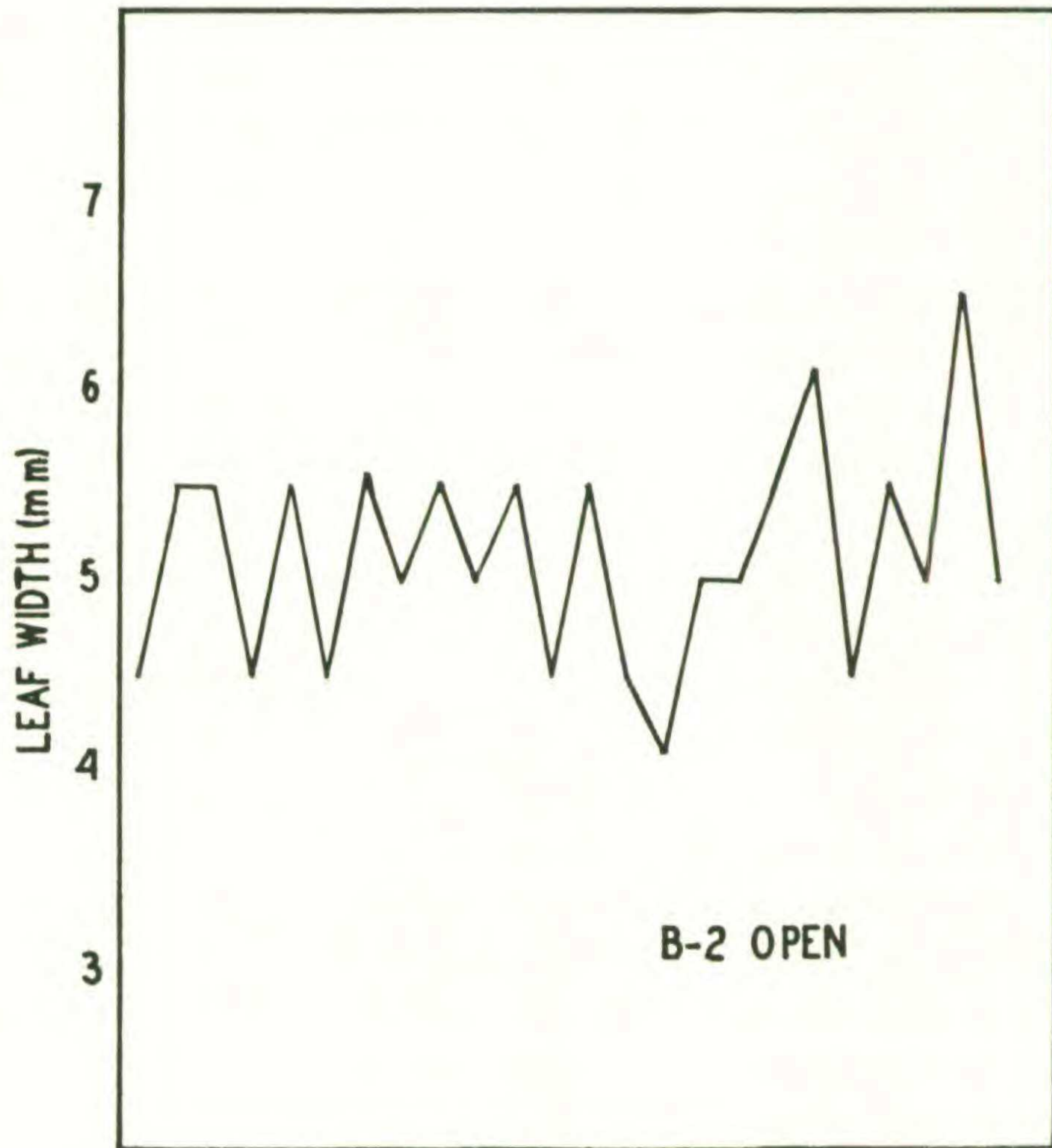


Fig. 1. Variation in leaf width in B-2 progeny after open-pollination.

to maturity and analyzed. Six of these progenies showed very marked differences in the number of aberrants occurring after selfing and after open-pollination, the selfed line always producing more variable types than the open-pollinated one. Strains which had previously been concluded to be apomictic behaved as sexually reproducing plants when they were isolated from foreign pollen. When segregation of a degree ex-



hibited by some of these selfed lines does occur it must be assumed that reproduction has taken place by gametic union. If this is true, what is there to prevent the open-pollinated lines of the same plant from functioning in a like manner? Assuming that the plant is potentially sexual, one might logically have expected the open-pollinated lines whose parents are sub-

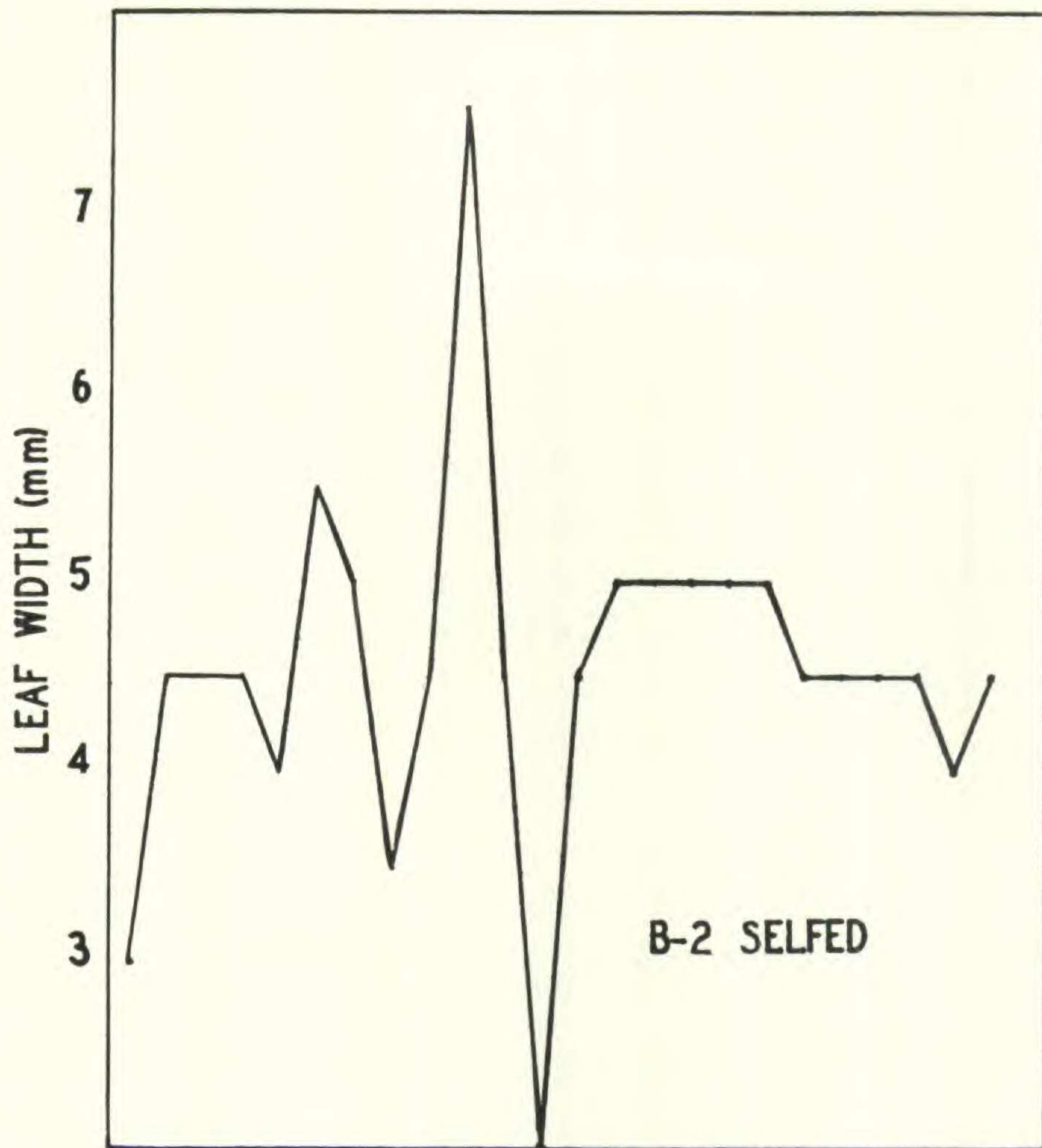


Fig. 2. Variation in leaf width in B-2 progeny after selfing.

ject to cross-pollination with other plants to exhibit more variation than the selfs. This, however, did not occur.

As a result of these analyses it is concluded that there are within *Poa pratensis* both sexual and asexual strains. Although the asexual strains are apparently predominant, the sexual ones occur frequently in most populations. Aside from purely sexual and purely asexual strains, there are those



plants which apparently reproduce asexually when open-pollinated but which reproduce sexually when selfed.

#### CHROMOSOME STUDIES

The polyploid nature of the genus *Poa* has long been established with 7 as the accepted base number. Within *Poa pratensis* somatic chromosome numbers range from 28, recorded by Avdulow ('31), to 110. This extensive polyploid series is not confined to euploidy, but a great many aneuploid numbers have been reported. The modal chromosome number for the species has been established as 56, Brown ('39). These 56-chromosome types are, for the most part, representative of average Blue grass, that is, they are of tall, upright habit, possess moderately narrow leaves, and average approximately three florets per spikelet.

Unfortunately, few correlated cytological and morphological data are available on *P. pratensis*. Müntzing ('40) makes some mention both of the cytology and morphology of some of the biotypes with which he has worked. Over a period of years I have observed that those low-growing plants with wide leaves, large spikelets, and heavy inflorescences have, with few exceptions, lower chromosome numbers than do those with narrow leaves, small spikelets, and average-size inflorescences. In fact, there is considerable evidence that approximately  $6n$  is the optimum for chromosome increase beyond which there is a marked decline in vigor.

In the present investigation no effort has been made to obtain even random chromosome numbers from a great many lots of plants. Instead, one lot was selected from which it was felt that chromosome data would be of particular significance. The great majority of progenies, after open-pollination, exhibited little, if any, variation and were eliminated as possible material for chromosome studies. After studying the morphological variability in G.S. Lot 5 it was immediately apparent that chromosome data from this progeny would be of special interest.

It will be remembered that the progeny of Lot 5, after open-



pollination, segregated into two distinct classes. Forty-five of the 55 plants were typical of the maternal parent while the remaining 10 were of a very different morphological type. Cytological examination of 35 of these plants has yielded some very interesting facts on the morphological effects of chromosome elimination from the original complement. The typical plants of the progeny, for the most part, possessed 49 somatic chromosomes (table II). The "off types," or aberrants, all of which belonged to a single morphological type, were, with one exception, shown to have 42 chromosomes, or one less genome than the typical plants. Thus the change from a moderately narrow-leaved, upright "hay" plant to a wide-leaved, low-growing one with increased vigor is the result of the elimination of one genome from the germ-plasm. The fact that all but one of the aberrant types contained one less genome instead of from 1 to 7 fewer chromosomes is of considerable interest. A number of  $2n$  plus 1-, 2-, or 3- or  $2n$  minus 1-, 2-, or 3-chromosome types have been investigated in other plants (*Zea*, *Datura*, etc.), and in most such cases the elimination or addition of even one chromosome was usually morphologically apparent. This, however, is not true in those plants of *P. pratensis* that have been studied. One of the typical plants (G.S. 5-5) possessed 47 chromosomes, yet it could not be morphologically distinguished from those with 49 chromosomes.

A few scattered chromosome counts have been made on plants selected from lots other than G.S. 5. Although these are so few that no conclusions can be drawn concerning the cytology of the lots as a whole, the following bit of information is of some interest. Lot 1, it will be recalled, produced a very low percentage of aberrants and is apparently an apomictic strain. Chromosome counts were made from six plants of this lot, and in all the  $2n$  number was found to be 56. Four out of five plants from Lot 2, another apomictic strain, were found also to possess 56 chromosomes. The number for the fifth plant could not be exactly determined but it was between 55 and 58. Lot 10, which reproduces at least partially by gametic union, yielded plants with 42, 41, and  $42 \pm 1$  chromosomes.



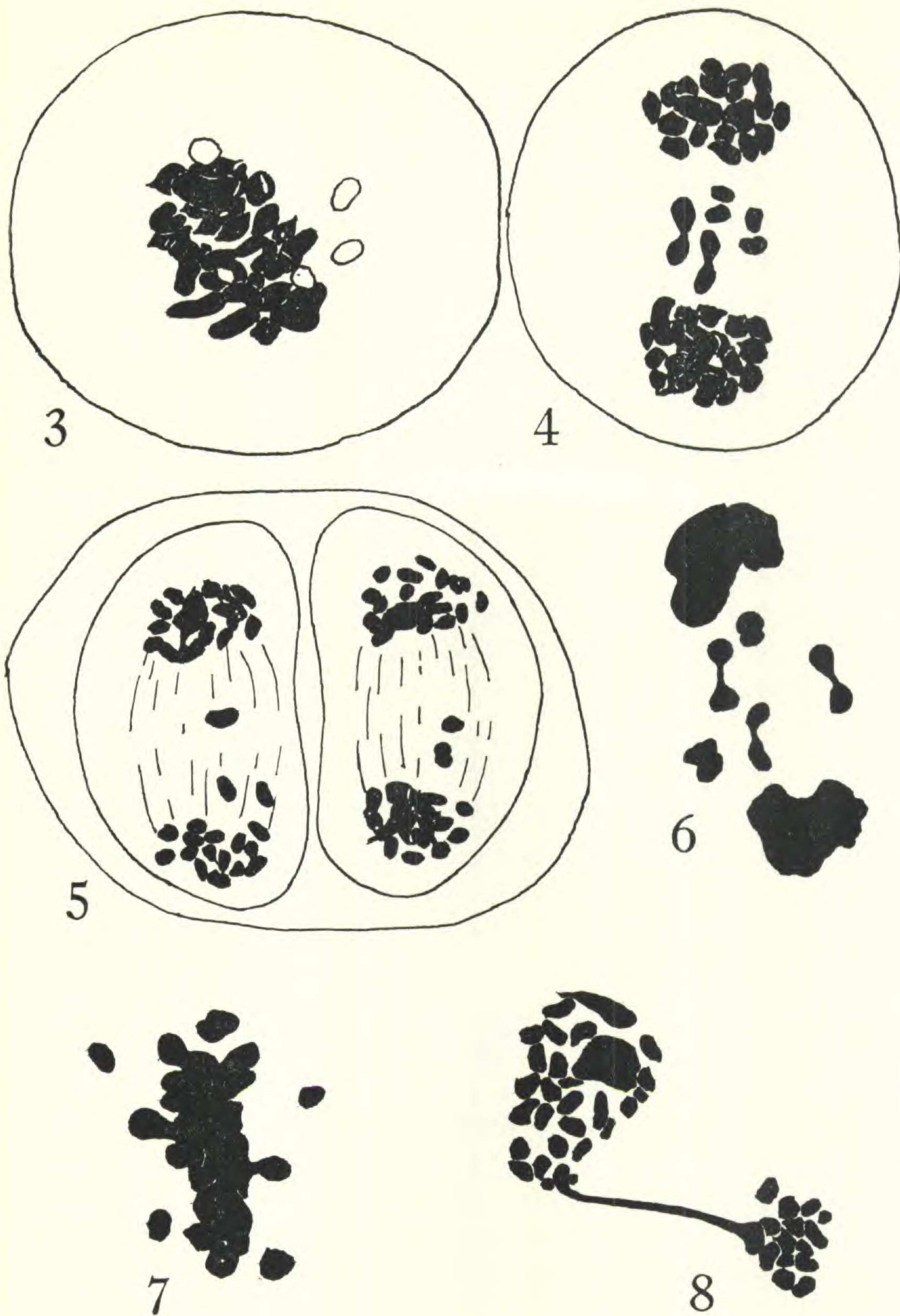
These data suggest that apomixis may be more prevalent in the higher chromosome types and that polyploids of approximately  $6n$  reproduce sexually.

TABLE II  
SUMMARY OF CHROMOSOME NUMBERS IN G.S. LOT 5

Plant	$2n$	Type of plant
5- 1	49	Typical
5- 2	42	Aberrant
5- 3	49	Typical
5- 4	49	Typical
5- 5	47	Typical
5- 6	49	Typical
5- 7	48-49	Typical
5- 8	48±1	Typical
5- 9	42	Aberrant
5-10	49-50	Typical
5-11	49	Typical
5-12	49	Typical
5-13	49	Typical
5-14	49	Typical
5-15	49	Typical
5-16	42	Aberrant
5-17	49	Typical
5-18	49	Typical
5-19	49	Typical
5-20	48-49	Typical
5-21	43±1	Aberrant
5-22	42	Aberrant
5-23	49±1	Typical
5-24	49	Typical
5-25	49-50	Typical
5-26	49±1	Typical
5-27	49	Typical
5-28	41-42	Aberrant
5-29	49	Typical
5-30	49	Typical
5-31	49	Typical
5-32	50	Typical
5-33	42	Aberrant
5-34	49-50	Typical
5-35	49	Typical

*Meiosis:* Observations on meiosis were made on a number of plants whose chromosome numbers had been previously determined somatically. Although meiosis in *P. pratensis* is not regular, the irregularity is not of a degree that might be expected in a highly polyploid species (figs. 3-13). Pairing is, for the most part, by bivalents, although univalents, trivalents, and quadrivalents have been observed in all cells examined.





Figs. 3-8. Camera-lucida drawings of meiotic chromosomes in *Poa pratensis*,  $\times 2000$ : fig. 3. Metaphase I from an apomictic plant showing 4 univalents, 3 trivalents, and approx. 23 bivalents, univalents in outline; fig. 4. Anaphase I from apomictic plant showing univalents dividing—not all polar chromosomes shown; fig. 5. Anaphase II showing lagging; fig. 6. Univalents dividing at Anaphase I, sexual plant; fig. 7. Metaphase I showing non-conjugation in apomictic plant; fig. 8. Anaphase I depicting unequal distribution with a dicentric chromosome.



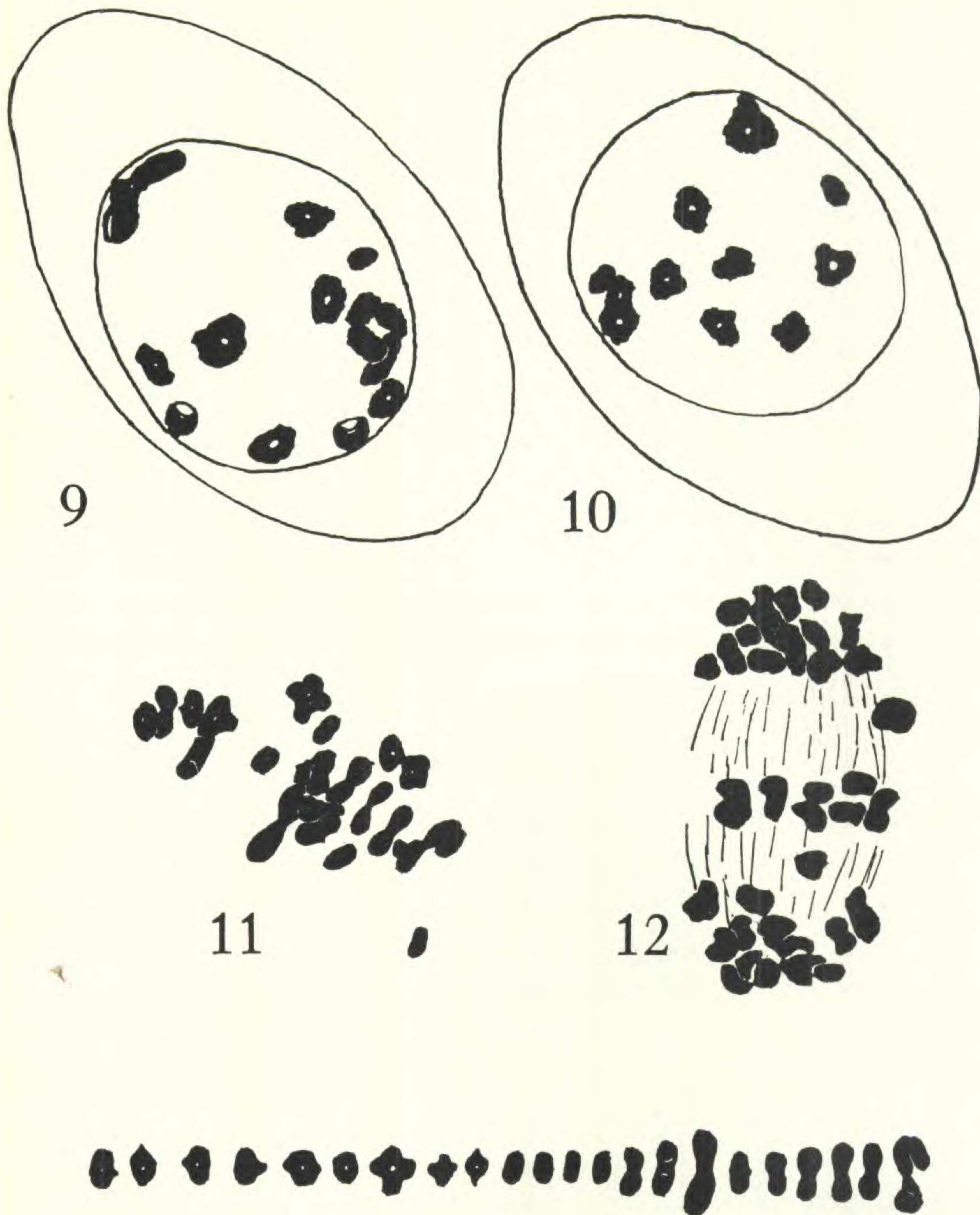
The majority of the bivalents are ring-shaped, averaging two chiasmata. Figure 11 represents a meiotic configuration which is rather typical of 42-chromosome plants. At Metaphase I the configuration consists of 17 II's, 4 I's, and 1 IV. At first anaphase most of the univalents divide after lagging in the region of the equatorial plate (fig. 12). The 56-chromosome plants show no more meiotic irregularity than do the hexaploids (fig. 3). The configuration at Metaphase I consists usually of 1-2 IV's, 1-2 III's, approximately 4 I's, with the remaining chromosomes paired as bivalents. Univalents usually lag at Anaphase I, but they always reach the poles in time to be included in one or the other of the polar groups. Distribution is, with very few exceptions, fairly equal at the anaphases. The tetrads and microspores appear to be normal, and micronuclei have not been observed in any of the cells examined. Some plants are obviously heterozygous for an inversion or duplication as indicated by the occasional occurrence of dicentric chromatids (fig. 8).

#### APOMIXIS

The occurrence of apomixis in *Poa pratensis* was first shown by Müntzing ('33). He studied a number of plants representing eight biotypes. A large percentage of his material was found to have aneuploid chromosome numbers, and for the most part the numbers within biotypes remained constant. Since the individual plants composing any one biotype exhibited little morphological variation, Müntzing assumed them to be apomictic. In a study of twin seedlings in *Poa pratensis* he ('37) found a rather high occurrence of polyembryony, which he considered to be in some way correlated with apomictic propagation. He states further that . . . "formation of 'triploid' twin plants, however, resulting from fertilization of unreduced ovules, demonstrates that apomixis in *Poa pratensis* is not absolute."

Åkerberg ('36) investigated seed production in eighty biotypes of *P. pratensis*. After employing both emasculation and free-flowering methods he concluded that pollination was nec-





Figs. 9-13. Camera-lucida drawings of meiotic chromosomes in *Poa pratensis*,  $\times 2000$ : figs. 9 & 10. Diakinesis in sexual plant, drawn in 2 planes—3 univalents, 16 bivalents, and 1 quadrivalent; fig. 11. Metaphase I from sexual plant showing 4 univalents, 17 bivalents, and 1 quadrivalent; fig. 12. Anaphase I from sexual plant showing lagging chromosomes—not all polar chromosomes shown; fig. 13. Metaphase chromosomes of fig. 11 drawn separately.



essary for seed production, but that pollen from *Poa alpina* had about the same effect as that from *P. pratensis*. For biotypes with aneuploid chromosome numbers and partial pollen sterility, Åkerberg postulated apomictic seed production. In a later investigation of progenies of *P. pratensis*, he ('39) attempts to determine the percentage of apomixis on the basis of morphological constancy. Of 703 plants investigated a little more than 90 per cent had the appearance of the maternal parents. These were assumed to be primarily apomictic and the 10 per cent of aberrants to be sexual. When 58 of the 703 plants were examined cytologically, 43 were found to have the same chromosome number as the mother plant; the remaining 15 were aberrants. Material was also collected from nature, and "of these 44 families, 37 were practically speaking morphologically constant."

Armstrong ('37) interprets the embryology of *P. pratensis* quite differently from the authors previously mentioned. Although he admits the occurrence of aneuploidy he still believes the species to be sexual and assumes that only gametes with certain chromosome numbers are capable of functioning. He has observed, in the embryo sac, a variation in the position of the functioning megaspore. This, he says, "provides a mechanism for the elimination of megaspores with an abnormal chromosome complement and for the choice of the megaspore containing the normal chromosome complement." On the basis of meiotic pairing he has assumed that 6/16 of the pollen would contain the normal chromosome complement, and he further states, "Assuming the same frequency of irregularity in megasporogenesis as in microsporogenesis, 6/16 of the megaspores would be normal, and with a choice of four megaspores the chance of obtaining one with the normal number is quite good."

Tinney ('40) found that the young ovules of *P. pratensis* always show a single, elongated, very conspicuous macrospore mother cell. The nucleus of this cell undergoes meiosis, and usually three haploid macrospores are formed, all of which subsequently disintegrate. The embryo sac arises from a cell



of the nucellus and when mature consists of three antipodals, a primary endosperm cell containing two nuclei and the egg apparatus. The diploid egg, according to Tinney, develops into a proembryo by parthenogenesis, the development beginning frequently before pollination. He did not observe endosperm development until after pollination and therefore concluded that pollination or the growth of pollen tubes in stylar tissue may be necessary for endosperm development and consequently seed development.

Tinney and Aamodt ('40) have analyzed 102 progenies of *Poa pratensis* in an attempt to arrive at the type of seed development in various biotypes. In 48 of them no variant types occurred, and these were thought to be apomictic. In one progeny, however, 21.9 per cent of the types were variant. These, it was thought, might have arisen through mutation or as a result of sexual reproduction.

Since all investigators of the mode of reproduction in *Poa pratensis* have shown that apomixis is one of the predominant factors involved, many have assumed that this phenomenon is of general occurrence within the species and can be taken advantage of in selection, etc. This assumption is to some extent undoubtedly true, but in view of the results obtained from this study it seems that we must distinguish between apomixis after selfing and apomixis after crossing or open-pollination.

*Apomixis after Open-Pollination:* It has been shown earlier that in lots B-2 and B-6 two very different types of progeny result when the same plants are selfed and allowed to produce seed without isolation. In plants reproducing by open-pollination the resulting progeny is essentially maternal-like morphologically and exhibit little, if any, variation within lines. Since *Poa pratensis* is an extremely diverse species it must, it seems, be assumed that constant morphological types of the nature just mentioned are being produced apomictically. The fact that foreign pollen must be present for the production of uniform progenies, however, is somewhat unusual and especially significant in the behavior of the species.

*Apomixis after Selfing:* If plants of strains B-2 and B-6 and



some other strains are isolated by bagging, progenies in direct morphological contrast to those obtained after open-pollination result. A wide range of variation both in vegetative and inflorescence characters usually results in these lines. Most of these strains segregate in a manner that would be expected only if the plant were reproducing sexually. These preliminary results indicate that in some strains of Kentucky Blue grass apomixis is dependent upon the presence of foreign pollen (pollen from another strain). The most logical hypothesis explaining the phenomenon is that the presence of foreign pollen on a stigma stimulates the development of some somatic cell of the embryo sac which, after the initial stimulation, goes ahead and functions as an embryo. Should the inflorescence of the same plant be bagged, thereby eliminating all foreign pollen, reproduction then takes place by gametic union (with the egg cell perhaps functioning normally). Besides explaining the differences in progeny obtained from the same plant after isolation and free-flowering, this hypothesis explains the varying but usually small percentage of aberrant forms present in most progenies of open-pollinated plants; i. e., they are the result of selfing, whereas the majority of the florets have received a stimulation from foreign pollen (as might be expected to occur in natural populations or in nursery rows).

The recent work of Englebert ('41) is very interesting in light of the results reported in this paper. Miss Englebert reports that in several species of *Poa*, including *Poa pratensis*, no endosperm was developed in emasculated, non-pollinated florets although embryos were found. She concluded, therefore, that the "germination of pollen on the stigmas stimulated the development of the aposporous polar cell to an endosperm (pseudogamy)." Although no embryological investigations have been attempted in the present study, the evidence from progeny analyses strongly indicates that in some strains of *P. pratensis* pollen plays a much more important role than the mere stimulation of endosperm development.

Several objections may be raised to the hypothesis just pre-



sented. For example, the increased temperature within a parchment bag might result in mutation and therefore in aberrant types. If this were true, however, one would expect comparable results in all selfed lines since the same methods of isolation were used in all plants investigated. As was noted earlier, this is not the case. Some strains, for example, B-6, produce nothing but uniform progenies regardless of whether or not the progenies are the product of isolation or open-pollination. As a further check on this point, three strains of *P. pratensis* which were thought to be apomictic were selected in 1940. Progenies of these were grown after (1) isolation by bagging, (2) isolation by caging, and (3) open-pollination. At maturity all three showed some slight random variation, but within any one strain there were no significant differences between plants produced under the different conditions. Yet in other selections which morphologically were almost identical with some of these lots, marked differences occurred in the number of variants produced after isolation and after open-pollination.

*Behavior of Apomicts in Generations beyond the F<sub>1</sub>:* In most instances the demonstration of apomixis in Blue grass has been the result of progeny analyses based on one generation of plants. As a result, few data are available on the behavior of the supposed apomicts beyond the first generation. For example, it is not definitely known whether or not a selection of *Poa pratensis* which produces a uniform progeny in one generation will continue to do so in following generations, yet, for practical purposes in seed production and strain improvement, this information is necessary. Records obtained from three selections of *Poa pratensis*, each of which has been maintained for three plant generations, shed some light on this problem. In each of these selections progenies have been studied from both selfed and open-pollinated lines.

*B-37.*—The plant from which this line was started is typical of “average” Blue grass, i. e., it is upright in habit, has narrow dark green leaves, average-size panicles, and produces an abundance of seed. The first-generation seedlings obtained after free-flowering were uniform and very similar to the ma-



ternal parent. However, approximately 15 per cent aberrant types occurred in the selfed lines, and these exhibited a rather wide range of variability. The second and third generations behaved essentially in the same manner. The open-pollinated lines were again constant morphologically while the selfs showed considerable variation.

*B-2*.—Although a different type of plant morphologically, the *B-2* progeny for three generations behaved very like that of *B-37*. The plants resulting from open-pollination showed no significant variation, although a number of "off types" occurred after selfing. These were, as a group, less vigorous and of a less desirable type than their parent. There were, nevertheless, a few exceptional cases in which promising segregates were obtained from selfed lines.

*B-30-19*.—In this strain, as in the two previous ones, asexual reproduction, resulting in uniform progenies, seems to function without change for at least three generations. In each generation, however, aberrant forms resulted from selfing.

TABLE III  
VARIATION IN PROGENY OF OPEN-POLLINATED LINES

Selection number	Per cent aberrants		
	1939	1940	1941
<i>B-37</i>	4.32	3.81	4.00
<i>B- 2</i>	1.63	3.21	1.71
<i>B-30-19</i>	0.09	0.09	1.04

These results indicate that in apomictic or otherwise asexually reproducing strains of *Poa pratensis* progenies may be grown or strains may be reproduced by seed without the interference of segregation in later generations. Deviation from type amounting to from 1 to 5 per cent of the total population would not likely have an undesirable effect on these selections when used in pasturage or turf. However, it cannot be assumed that all *Poa pratensis* will behave in a manner exhibited by selections *B-2*, *B-37*, and *B-30-19*. As was shown earlier, G. S. Lot 5 and G. S. Lot 10 produce approximately 20 per cent



aberrants in progenies resulting from open-pollination. Deviations of this magnitude would soon result in a heterogeneous mixture if attempts were made to reproduce the types from seed.

#### DISCUSSION

Amphimixis results in many and varied gene combinations and hence in an increased genetic morphological variability, but, due to a variety of both internal and external causes, only a small per cent of the gene combinations produced in any sexually reproducing species survives. As a result the majority of plant species remain more or less constant from generation to generation. There are, however, in the plant world a great many groups whose variability makes the delimiting of species exceedingly "difficult." It is interesting to note that the majority of these groups are those in which asexual reproduction is the predominant mode of propagation (Dobzhansky, '37). Under such a system any genetic change occurring within a species is not usually eliminated as it might well be if the species were sexual, but instead it is maintained and propagated vegetatively as a new clone. This soon develops into a variety of forms, a so-called "species complex." In *Poa pratensis* this condition is further accentuated by the operation of both amphimixis and apomixis within a single strain. Although evidence from progeny analyses indicates that the great majority of *Poa pratensis* strains reproduce normally by apomixis, in each of the progenies studied from 0.9 to 18 per cent of the offspring were found to be the product of sexual reproduction. In nature a great many of these "new" strains would be eliminated due to their inability to compete successfully with other strains, but a number of them might be expected to survive and these will, in many instances, further propagate their kind through apomixis. Thus it is evident that *Poa pratensis* is equipped not only for producing new or aberrant types but is especially well equipped for propagating these types vegetatively through seeds once they do occur.

Since both sexual and asexual reproduction have been demonstrated in *Poa pratensis*, information on the factors affect-



ing apomixis is a prime prerequisite to any strain-improvement program. However, little information is available on the causes of a breakdown in the sexual reproducing system in plants. Darlington ('37) has shown that when such a breakdown does occur it is usually replaced by some form of asexual reproduction. It has been further suggested that asexual reproduction may be the result of hybridization since many apomicts are known to be of hybrid origin. This is a possibility in *P. pratensis* which might well have originated as an allopolyploid hybrid.

Brown ('40) has shown that, despite the extreme variation exhibited by *P. pratensis*, there is a more or less constant grouping of all variables into two main complexes. One includes plants with wide leaves, many florets per spikelet, long and wide panicles, and many panicle branches. Into the other complex fall those plants with narrow leaves, few florets, short and narrow panicles, and few panicle branches. Regardless of what characters are considered or to what degree the variability may occur, the varying units always tend to group themselves into one of these two complexes. This suggests strongly that in the germ plasm of *P. pratensis* there are at least two entirely different elements. While it might be suggested that the differences between strains are a result of changes within the germ plasm, crossing-over, translocations, inversions, interchanges, etc., such differences would tend to occur at random and not in the distinct groups which have been demonstrated. It is impossible to prove conclusively the allopolyploid nature of *P. pratensis* without reproducing it artificially. Nevertheless, all its peculiarities point to a probable hybrid origin. Whether or not hybridization can be shown to be a basis for apomixis remains to be seen, but at least *P. pratensis* is another example of an apomictic species whose behavior is essentially that of a hybrid.

*Chromosome Numbers and Apomixis:* The correlation between per cent apomicts and chromosome number as exhibited in the G.S. plants is very interesting and perhaps significant. It will be recalled that in G.S. Lot 5 the chromosome numbers



were found to be either approximately 42 or approximately 49. This progeny contained 18.18 per cent aberrants. Likewise, G.S. Lot 10, containing 16.66 per cent aberrants, exhibited chromosome numbers of 42 and approximately 42. In contrast, six typical plants from Lot 1 and five from Lot 2 were found to have  $2n$  numbers of 56. These lots yielded 1.50 and 0.97 per cent aberrants respectively. Although this evidence is not conclusive it does indicate that apomixis tends to increase as chromosome number increases. The evidence for a hybrid origin in the 42- and 49-chromosome plants is just as pronounced as it is in the octoploids. Therefore, according to these data, it must be assumed that chromosome duplication (perhaps following hybridization) is at least one of the factors affecting apomixis. On the other hand, it is not likely that any one or any few factors govern the operation of apomixis in *Poa*. Indeed, the isolation experiments suggest that the presence or absence of foreign pollen has a very marked effect on the functioning of asexual reproduction.

*Genetics of the Various Genoms:* Perhaps the most important contribution contained in this paper concerns the morphological effect of a duplication or elimination of chromosomes within a single strain. It is only logical to expect differences in morphological characters to be correlated with differences in chromosome numbers. Since, however, *Poa pratensis* is exceedingly variable both morphologically and cytologically and since it is not a plant which lends itself well to cytological study, in the past it has been difficult to arrive at any conclusion regarding the morphological effects of the addition or elimination of one or more genoms of the germ plasm. Two lots of G.S. plants, G.S. 5 and G.S. 10, have afforded an excellent opportunity for a study of this sort. These progenies, it will be recalled, segregated into two quite clear-cut types. The tall, upright one possessed narrow leaves and closely resembled the parent, while the second type was in direct contrast to the parent morphologically. The  $2n$  number of the first type was 49, that of the second 42.

From these data two facts are evident. First, at least two



types of *P. pratensis* can be transformed into entirely different types morphologically by the addition or elimination of one set of chromosomes. From the practical standpoint this knowledge should be of considerable importance to those interested in producing Blue grass for specific purposes. If one could predict with reasonable accuracy the types of Blue grass expected to segregate from certain selected strains, a great many of the initial difficulties encountered in strain improvement would be eliminated. Second, at least some unstable chromosomal types may revert to more stable and potentially sexual forms. Thus, the odd-numbered 49-chromosome plants which would be quite unstable upon cross-fertilization have produced 42-chromosome plants whose chromosomal stability could be maintained regardless of whether reproduction takes place by sexual or asexual methods.

On the basis of these observations the extreme diversity of *Poa pratensis* can be fairly well explained, and our knowledge of the factors affecting the behavior of the species, although still not complete, suggests a number of new approaches to the problem. The presence of a long euploid series within *P. pratensis* results in considerable variation. The various odd-chromosome forms, most of which are being maintained asexually, more than double this original variation. The complexity is further accentuated by the simultaneous operation of apomixis and sexual reproduction within single strains and the ability of unstable chromosomal types to revert to potentially sexual forms.

#### SUMMARY

In eleven lots of plants of *Poa pratensis* grown from seed produced by open-pollination, aberrant types amounting to from 0.09 to 18.18 per cent of the populations have been observed within strains. Although the majority of progenies contained from 1 to 5 per cent aberrants, two partially sexual strains produced 16.66 and 18.18 per cent off types. In one lot which was investigated in detail the chromosome number of the maternal-type seedlings was 49, that of the aberrants 42.



In some strains of *P. pratensis* the behavior of progenies after bagging and open-pollination is very different. Certain strains which after open-pollination produce uniform, maternal-like progenies may after bagging produce highly variable progenies which are apparently the products of gametic union. To explain this phenomenon, an hypothesis is offered based on an apomictic stimulating effect of foreign pollen.

In certain of these cultures the transition from a typical "hay" type *Poa pratensis* to a low-growing, wide-leaved spreading type of plant was brought about by the loss of one genom from the germ plasm. It is further shown that chromosome complements composed of odd-numbered chromosome sets may segregate into stable even-numbered chromosomal types.

Apomixis and the factors affecting this type of reproduction are discussed in the light of the results of this investigation. Evidence is presented which shows that apomixis is more prevalent in high polyploids than in those strains characterized by lower chromosome numbers. It is suggested that *Poa pratensis* may have originated as an allopolyploid, partially apomictic hybrid.

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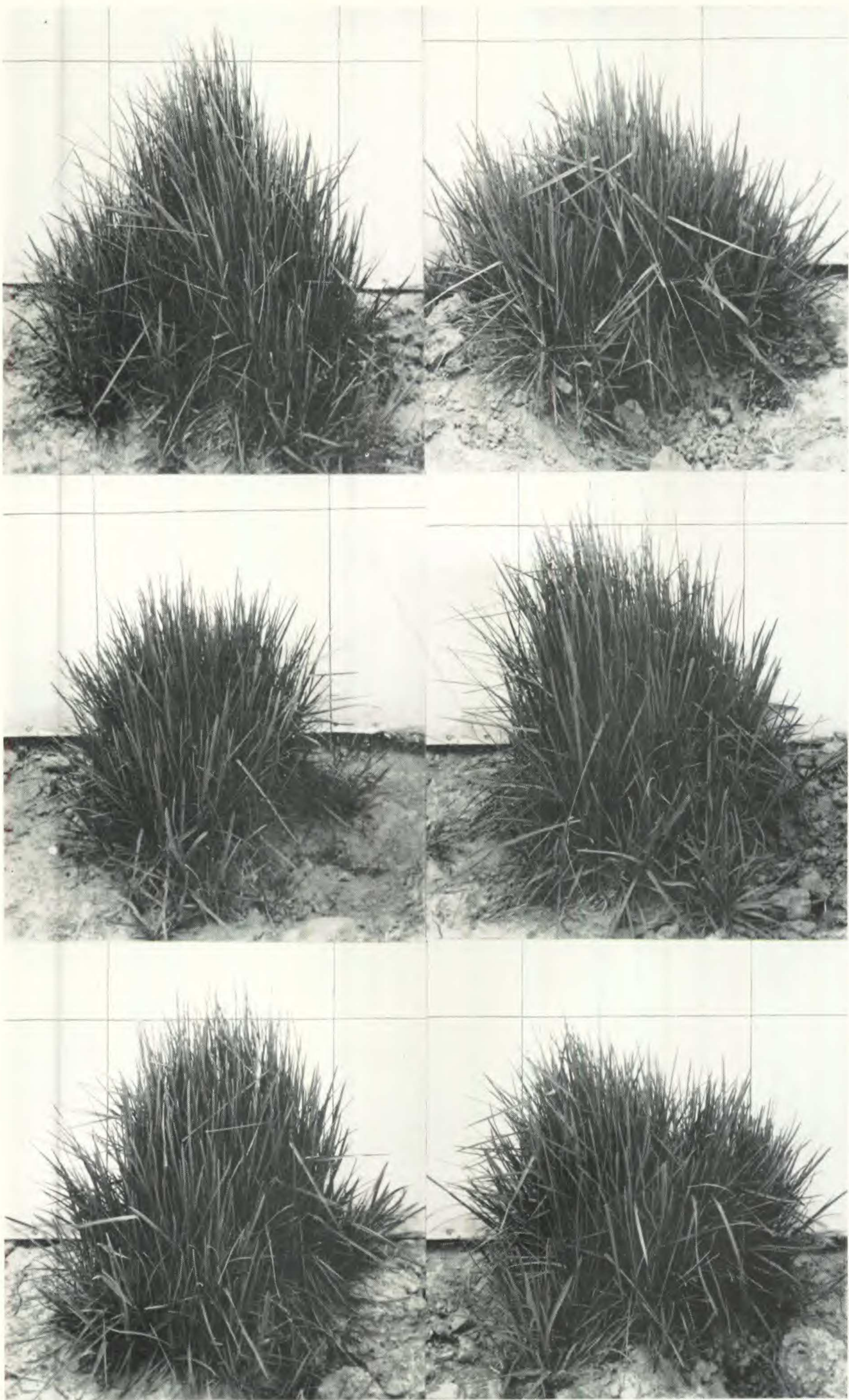
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## EXPLANATION OF PLATE

## PLATE 26

Selection B-1. Typical representatives of progeny resulting from open-pollination. Compare with plate 27.





BROWN—CYTOGENETICS OF POA PRATENSIS

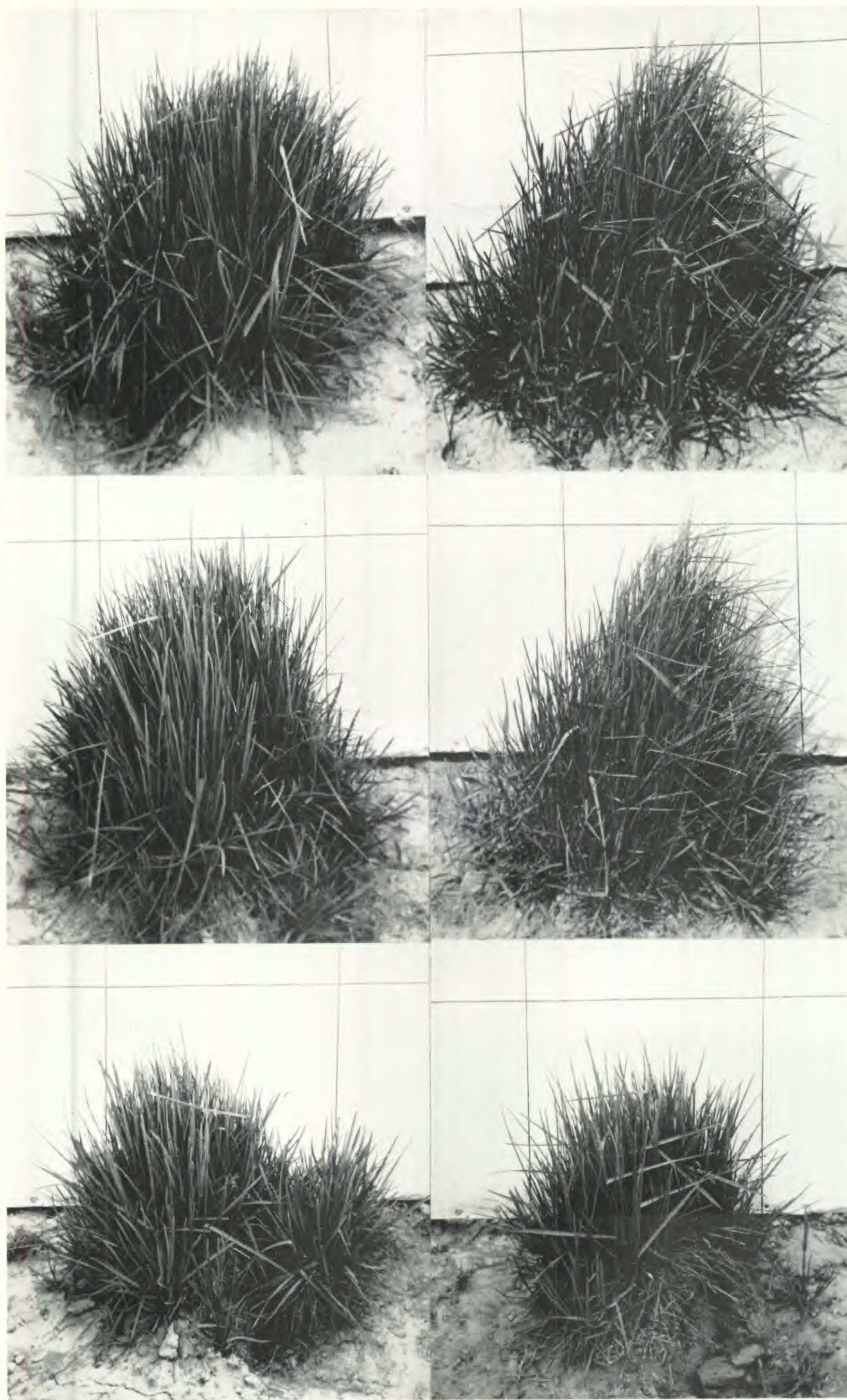


## EXPLANATION OF PLATE

## PLATE 27

Selection B-1. Typical representatives of progeny resulting from selfing. Compare with plate 26. All plants shown in plates 26 and 27 are progeny of the same maternal parent.





BROWN—CYTOGENETICS OF POA PRATENSIS

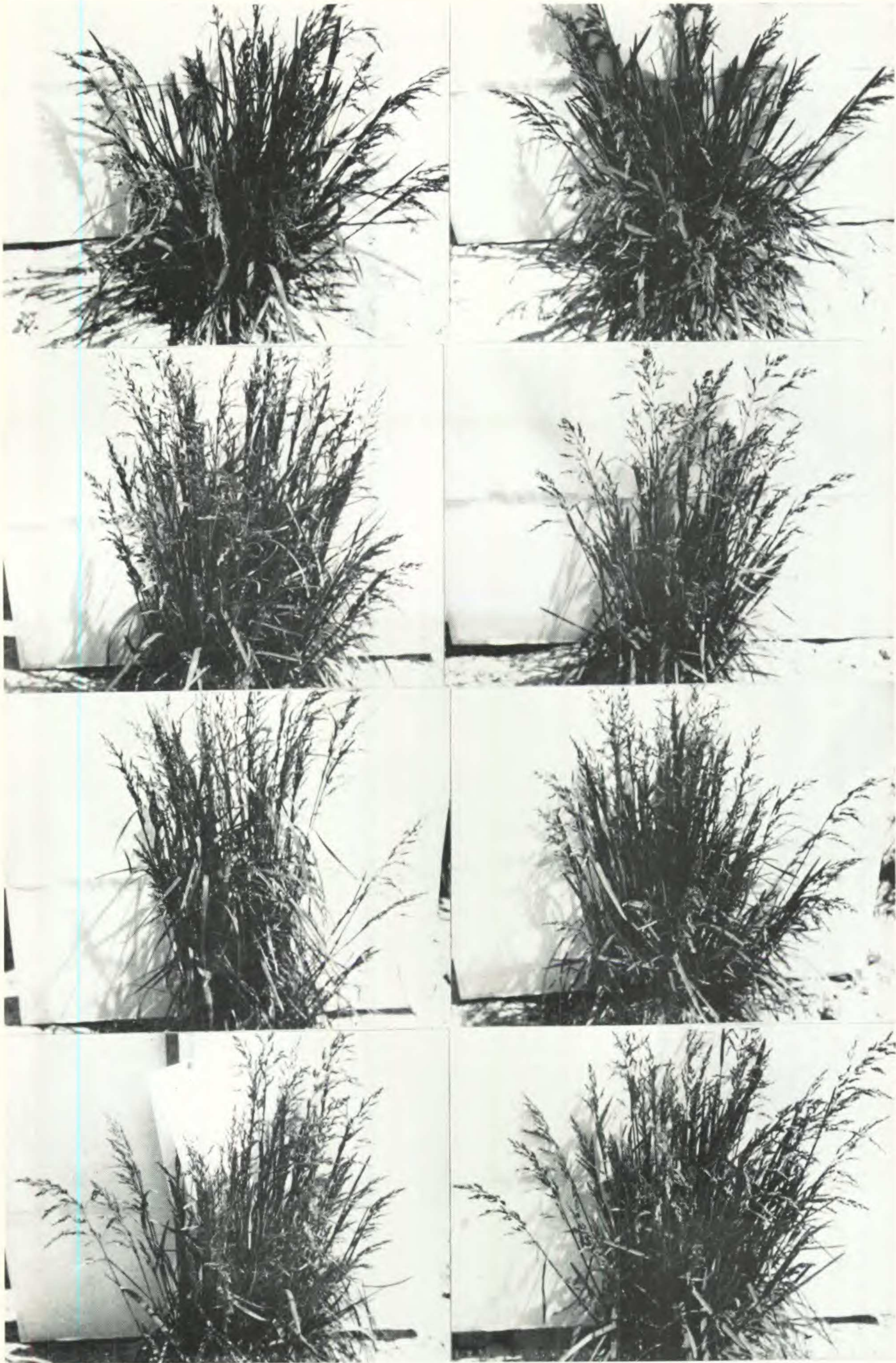


## EXPLANATION OF PLATE

## PLATE 28

Selection B-6. Typical representatives of progeny resulting from open-pollination. Compare with plate 29.





BROWN—CYTOGENETICS OF *POA PRATENSIS*



## EXPLANATION OF PLATE

## PLATE 29

Typical representatives of progeny resulting from selfing. Note the variability and low, spreading habit of these plants as compared with those shown in plate 28. All plants shown in plates 28 and 29 are progeny of the same maternal parent.